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ALLOGNATHOSUCHUS MOOKI, A NEW CROCODILE FROM THE PUERCO FORMATION

BY GEORGE GAYLORD SIMPSON

One of the principal discoveries of the 1929 expedition of the American Museum of Natural History to the San Juan Basin, New Mexico, was the nearly complete skeleton of a crocodile. The specimen is interesting morphologically because it reveals the complete osteology in a peculiar phylum hitherto known only from fragments; faunally, because it is the first good and really identifiable crocodile material from the Paleocene; stratigraphically, because it adds an important example to the very few lines that do or may give some conception of actual evolutionary advance in the Cretaceous-Tertiary transition; and ecologically, because it is a peculiar adaptive type hitherto misinterpreted.

Complete description of the specimen, not yet fully disarticulated and cleaned, falls within the province of Mook's monographic studies on the living and extinct Crocodilia, now in progress, and the present notice will be followed by his more detailed morphological account.

TAXONOMY

No crocodiles from the Paleocene have hitherto been named or identified. *Crocodilus stavelianus* Cope, 1885, is generally given as from the Puerco, but the original description clearly states that the type was associated with dinosaurs and came from the "Laramie." It is indeterminate, furthermore, and the single type tooth does not agree with any in the present specimen.

Gilmore (1920) noted the presence of crocodiles in the Puerco and Torrejon, but stated that his material was indeterminate. Mook (1921A) said that teeth like those of *Allognathosuchus heterodon* (a Wasatch species) occur in the Puerco and that this genus might be present in the Paleocene. The existence of Paleocene crocodiles has long been known, but their morphology and affinities are almost completely unknown or unpublished.

The present specimen belongs in the genus *Allognathosuchus*, as will be made clear below. It is placed in a new species named in recognition

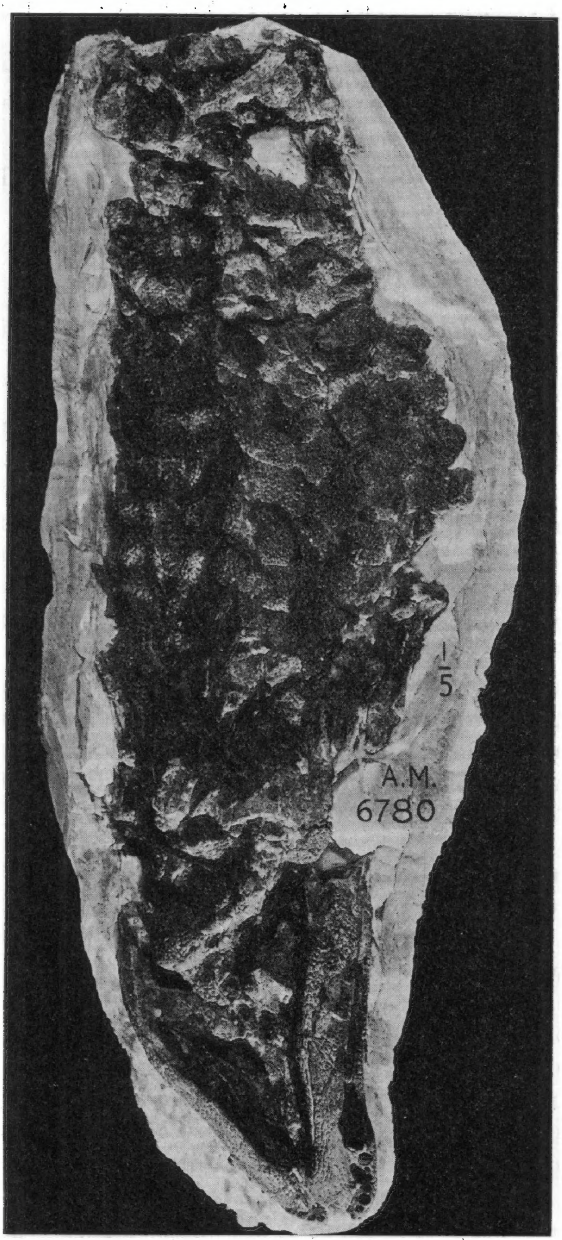

Fig. 1. *Allognathosuchus mooki*, n. sp. Type, Amer. Mus. 6780. Skull and part of skeleton showing scutes. Inferior view. One-fifth natural size.

of Dr. C. C. Mook's extensive work on Crocodilia and first distinction of the genus of which this becomes the most complete representative.

Allognathosuchus mooki, new species

TYPE.—Amer. Mus. No. 6780, skull, jaws, and most of skeleton. Coll. G. G. Simpson, 1929.

HORIZON AND LOCALITY.—Upper fossil level ("*Tæniolabis* zone"), Puerco Formation, Barrel Spring Arroyo, San Juan Basin, New Mexico.

DIAGNOSIS.—The earliest known species of *Allognathosuchus*. Size relatively large, skull somewhat more elongate, less distinctly triangular than in *A. heterodon*. Five premaxillary, fourteen maxillary, and twenty mandibular teeth. Third and fourth maxillary and fourth and thirteenth mandibular teeth much enlarged, conical. Third maxillary teeth larger than in *A. heterodon;* posterior upper teeth somewhat less enlarged and bulbous. Lower jaw very stout, dental border depressed and flattened, symphysis deeper than in *A. polyodon*, surangular rising less abruptly posterior to teeth, alveoli separated by stouter, more complete walls.

The diagnosis of species is difficult, as the genus is not much varied and the later species are poorly known. The specific characters of *A. polyodon* and *A. heterodon* as given by Mook (1921A) are for the most part generic and not specific, or at least appear, so far as known, in both of these species, in *A. mooki*, and probably also in *A. wartheni*. The discrepancies in the description of the latter (Case, 1925) are that the thirteenth to fifteenth mandibular teeth (by our count) are said to be equal and that there would apparently be two less posterior lower teeth. From Case's figures and text no greater difference than this can apparently be postulated, and the material is so fragmentary that the reality of these distinctions is not wholly clear. The specific status may well be granted on Case's authority, however, and it seems that *A. wartheni* cannot be compared with *A. mooki* as closely as can its contemporary *A. heterodon*.

The generic characters may be briefly emended as follows:

Allognathosuchus Mook, 1921

TYPE.—*A. polyodon* (Cope, 1873).

REFERRED SPECIES.—*A. heterodon* (Cope, 1872); *A. wartheni* Case, 1925; *A. mooki* Simpson, 1930.

DISTRIBUTION.—*A. polyodon*, Bridger, Wyoming. *A. heterodon* and *A. wartheni*, Wasatch, Wyoming. *A. mooki*, Puerco, New Mexico.

DIAGNOSIS.—Crocodilidæ of small to medium size. Skulls short and broad, snout short, blunt. Nasals entering but not dividing external nares. Internal nares relatively anterior. Supratemporal fenestræ about half as large as orbits, relatively close together. Symphysis short, but including splenials. Postdental part of lower jaw longer than dental. Upper border of lower jaw wavy, rising anteriorly, in the vicinity of the thirteenth tooth, and posterior to the teeth, and concave between these

elevations. Bite alligator-like, the anterior lower teeth occluding altogether internal to the upper teeth and to the edge of the palate, the posterior lower teeth partly internal and partly opposed to the uppers. Dentition differentiated into anterior conical

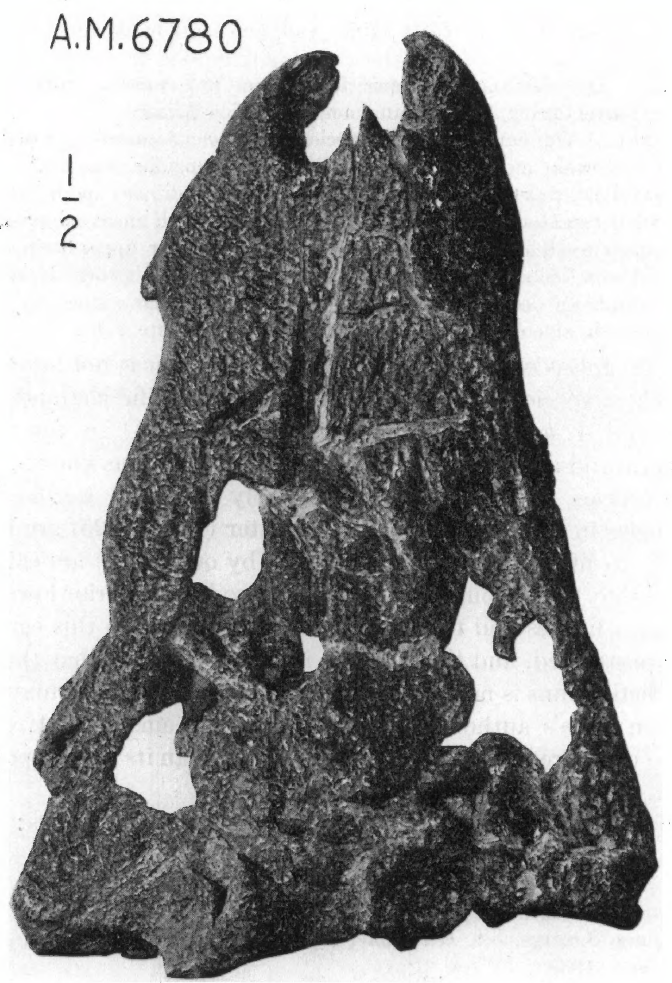

Fig. 2. *Allognathosuchus mooki*, n. sp. Type, Amer. Mus. 6780. Skull, superior view, one-half natural size.

teeth and posterior blunt, globose, low-crowned teeth. Two much enlarged conical teeth in lower jaw (often or always the fourth and thirteenth) separated by a series of very small subspatulate or conical teeth. One or two much enlarged conical teeth in upper jaw (fourth or third and fourth maxillary teeth).

MORPHOLOGY

Complete morphological description by Dr. Mook will follow. The present section is confined to brief notes on certain features of interest in the skull, jaws, and dentition.

SKULL.—The general form of the skull is alligatoroid, the outline most nearly resembling *Jacare niger* among recent crocodilians. The contour of the blunt snout is broken by swellings for the large third and fourth maxillary teeth and by shallow notches posterior to these. The snout is depressed, with no preorbital crests or elevations, and the braincase rises moderately above it. The total length of the skull is about 235 mm., the preorbital length about 117 mm., and the maximum preorbital width 110–115 mm., as nearly as measurable on the crushed specimen.

The orbits are about 55 mm. in diameter and are open into the infratemporal fenestræ. The interorbital region and cranial table are but slightly concave. The supraorbital fenestræ were about 30 mm. in diameter, the outer bars about 17 mm., and the middle bar about 15 mm.

The external nares are at the tip of the snout, the anterior processes of the premaxillæ being narrow and but slightly reflected back over the nares. The nares are undivided, but the tips of the nasals project into them. The nasals are long, lanceolate together, and extend nearly to the level of the orbits. The frontals were not inserted between them.

The palatines extend well forward of the posterior palatal vacuities, and their anterior parts are distinctly wider than between the vacuities. The internal nares are removed about 13.5 mm. from the vertical posterior pterygoid-basisphenoid plate—a remarkably anterior position.

These and other osteological characters of the skull seem to be fairly close to the typical primitive true crocodilid condition. The other modifications are of minor significance and mostly related to the unusual proportions: short dental series and long postdental region.

LOWER JAW.—The more important features of the lower jaw have been described by Mook for *A. polyodon*. That of the present species is similar save in detail. The symphysis, deeper than in *A. polyodon*, extends to about the eighth mandibular tooth and includes the splenials for a short distance. The jaw is stouter than in *A. polyodon*. The dental border is flattened and forms a shelf internal to the first thirteen teeth and on both sides of those behind this point. Opposite the last four teeth it forms a sharp flange projecting above the inner surface of the jaw. The rise posterior to the teeth is not as marked in the present species, and its abruptness is exaggerated in Mook's photographs and subsequent restorations of *A. polyodon* because the sloping anterior end of the surangular is broken off in that type specimen. The mandibular foramen, absent in Case's restoration and small in Abel's, is of average size in the present specimen and was apparently similar in *A. polyodon*.

DENTITION.—There are nineteen upper and twenty lower teeth on each side. Five of the upper teeth are in the premaxilla and fourteen in the maxilla.

The crowns of the premaxillary teeth are not preserved. The alveoli are approximately circular and increase in size to the fourth, the first and fifth being about equal. They are closely spaced, but separated by stout, complete walls. At the premaxillo-maxillary suture there is a short diastema of about 6 mm.

The first maxillary alveolus is small. The crowns of the second to fourth teeth are preserved and are of the normal conical, carinate, slightly recurved crocodilian type with faintly wrinkled enamel. The second is small, but the fourth is the largest tooth in the entire dentition, and the third is but little smaller. The next three alveoli,

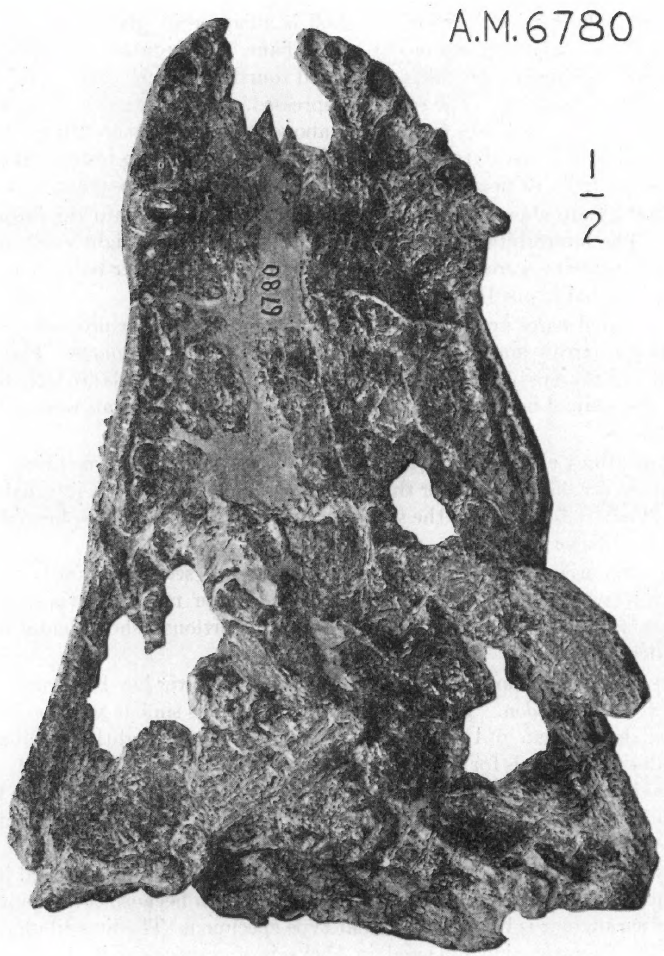

Fig. 3. *Allognathosuchus mooki*, n. sp. Type, Amer. Mus. 6780. Skull, inferior view, one-half natural size.

fifth to seventh of the maxilla, are subcircular and with stout, complete partitions. There follows a series of seven teeth more closely crowded, somewhat elongate anteroposteriorly, with the alveolar partitions incomplete toward their mouths. These teeth, eighth to fourteenth of the maxilla, increase in size to the twelfth; the thirteenth

is slightly and the fourteenth considerably smaller. The crowns of the last three are preserved on one side and are of the *Allognathosuchus* type described by Mook and Case: low, rounded, button-like, with radiating rugosities and an anteroposterior carina but no elevated apex.

The diameters of the alveoli vary somewhat with stage of replacement and are not exactly mensurate, but are about as follows:

Premaxillary:	1– 4 mm.	
	2– 5	
	3– 6	
	4– 9	
	5– 4	
Maxillary:	1– 4	8–5
	2– 5	9–6
	3– 9	10–6.5
	4–13	11–8
	5– 5	12–9
	6– 4	13–9
	7– 4	14–4

The lower dentition begins in front with a moderate-sized conical tooth followed by two others (roots only on the specimen) slightly smaller. The fourth is very large and similar to the fourth maxillary tooth. The teeth in the concavity between this and the next elevation of the dental border cannot be exactly counted on the type, but in another specimen found in 1929 there are eight, which agrees with *A. polyodon.* These are all very small except for the eighth (twelfth of the whole series) which is of moderate size. The crowns of some of these are preserved. They are not depressed, but are subspatulate rather than sharply pointed, with sharp anterior and posterior carinæ, and with the outer side more convex than the inner.

The median elevation in the lower dental series bears the thirteenth tooth, which is large and conical, and the fourteenth, smaller but probably similar. Judging from a Wasatch specimen of *A. heterodon,* the next two alveoli contained teeth transitional in form between the conical and hemispherical types. The last four teeth are preserved and form a depressed, crushing series comparable to the last teeth of the upper jaw. The most anterior preserved has a low but definite apex, while the others are still more flattened.

The large fourth mandibular tooth fits into a deep pit internal to the last premaxillary and first two maxillary teeth, through the bottom of which the suture passes. The thirteenth mandibular tooth fits into a similar but smaller pit internal to the sixth and seventh maxillary teeth. Anterior and posterior to this are very small and poorly defined depressions for the twelfth and fourteenth lower teeth.

Approximate alveolar diameters follow. Those for the fifth to eleventh are from another specimen:

1– 5	5–4	9–3	13–8	17–6
2– 4	6–4	10–3	14–6	18–7
3– 4	7–3	11–4	15–4	19–9
4–11	8–3	12–6	16–5	20–8

Fig. 4. *Allognathosuchus mooki*, n. sp. Type, Amer. Mus. 6780. Jaws, superior view, one-half natural size.

AFFINITIES

It is evident that the present species is referable to *Allognathosuchus*. The differences from *A. heterodon* and *A. wartheni* of the Wasatch and from *A. polyodon* of the Bridger are of specific value, but the four species form a closely delimited group, perhaps a phylum in the most limited sense of the word, although not all of its progressive features can yet be clearly ascertained. They are not very closely comparable to any other known crocodiles.

Further comparisons may exclude Lower Cretaceous or earlier genera and be confined to short-snouted, more or less alligatoroid types. Thus the forms especially to be considered are *Brachychampsa montana* Gilmore of the late Cretaceous, *Caimanoidea*[1] *visheri* Mehl and *C. prenasalis* (Loomis), of the Oligocene, and *Alligator thomsoni* Mook of the Miocene.

Brachychampsa Gilmore, 1911, from the Hell Creek of Montana, is the only known Cretaceous genus with which close comparison is possible. It is known from the front part of the skull. The general proportions are similar to those of *Allognathosuchus*, and so are the general osteological features. Differences are seen in the probably larger facial processes of the premaxillaries, their less reflected anterior borders, the less marked constrictions of the snout, and the much shallower palatal pits. The number of teeth in premaxillæ and maxillæ is the same, but their proportions and forms are not in close agreement. The premaxillary teeth of *Brachychampsa* are more nearly equal in size, and the third is somewhat larger than the fourth. The first five maxillary teeth are subequal, but the fifth, rather than the fourth, is the largest. The following teeth have somewhat the proportions of *Allognathosuchus*. The larger posterior teeth have a special resemblance to those of *Allognathosuchus* but have less depressed crowns. The twelfth maxillary tooth of *Brachychampsa montana*, figured by Gilmore, rather closely resembles the ninth maxillary tooth of *Allognathosuchus heterodon*, for instance, but is larger and has a somewhat higher crown.

Brachychampsa and *Allognathosuchus* trend toward similar adaptive types. The differences are too great and the elapsed time between them too short for possible direct ancestry or very close relationships. The known resemblances are insufficient for final conclusion, but might be interpreted by a tentative hypothesis of rather remote common ancestry. The direct ancestry of *Allognathosuchus* is unknown.

The morphological relationships between *Allognathosuchus* and *Caimanoidea* are unusual. Were *Caimanoidea* the earlier genus, one might suppose it approximately ancestral, for many of its peculiarities resemble those of *Allognathosuchus* but are less extreme. The position and shape of the nares are the same, save that in *Caimanoidea* (as in *Brachychampsa*) the anterior ridges on the premaxillæ are less reflected. The nasals are similar and likewise project into but do not divide the nares. The orbits are closely similar, the supratemporal fenestræ rela-

[1]This name is spelled in three different ways in Mehl's paper (Mehl, 1916); I presume the present spelling was intended.

tively smaller and farther apart. The interorbital and preorbital regions are similarly flat and uncrested. The snout contour is closely similar, with a slight premaxillo-maxillary and pronounced maxillary constriction. The skull is somewhat less triangular in general form than in *A. mooki* and much less than in *A. heterodon*. Most of the other observed osteological characters are the same or similar.

The lower jaw of *Caimanoidea* differs from that of *Allognathosuchus* in the relatively shorter post-dental portion and less pronounced eleva-

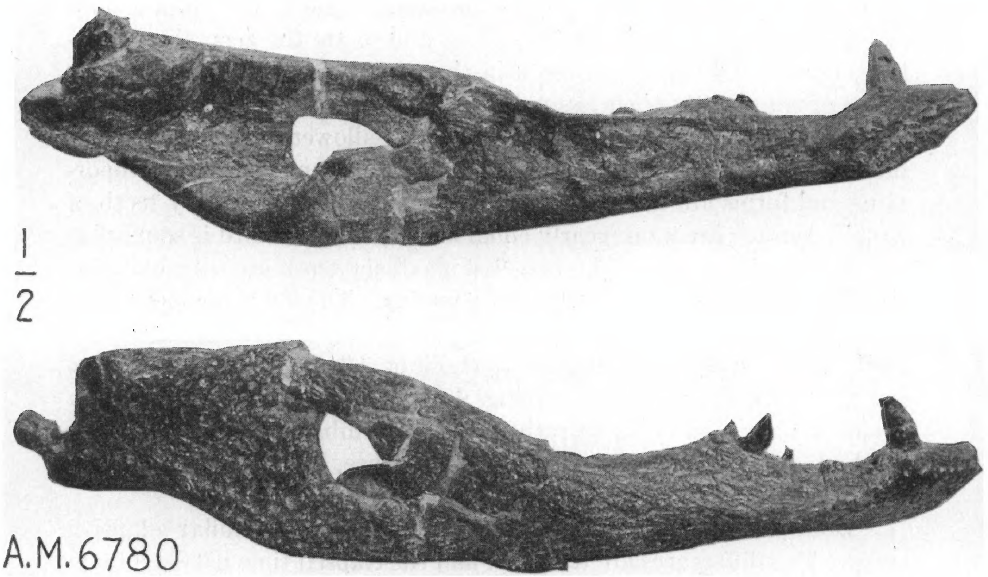

Fig. 5. *Allognathosuchus mooki*, n. sp. Type, Amer. Mus. 6780. Jaws. Upper figure: left ramus, internal view. Lower figure: external view. Both figures one-half natural size.

tion in the middle of the dental series. It agrees in the most noteworthy feature, the strong participation of the splenial in the symphysis.

The dentition likewise has points of important resemblance, but in several respects it seems less specialized in the later genus. The number of maxillary teeth is one less, and so is the number of mandibular teeth. As in *Allognathosuchus*, the fourth premaxillary tooth is the largest of this series and the fourth maxillary tooth is the largest of the whole dentition. Also the anterior teeth are conical and the posterior teeth depressed, with constricted necks and indistinct carinæ. They are not as much flattened as in *Allognathosuchus*, but the difference is not very great and

the general proportions are similar. The lower dentition continues the resemblance. The fourth tooth is likewise largest and bites into a deep pit on the premaxillo-maxillary suture. Still, as in *Allognathosuchus*, the first tooth is larger than the subequal second and third. The resemblance even extends to the presence of seven very small teeth in the concavity posterior to the fourth. The median convexity and the large thirteenth tooth are less differentiated, however, and the posterior teeth, like those of the upper jaw, are less extremely depressed.

I do not think it possible to dismiss these resemblances as due entirely to convergence. They are more numerous and more specific than in the case of *Brachychampsa*, for instance. Aside from a few divergent or indifferent characters, however, it is fairly clear that *Caimanoidea* is the more primitive in most of the known parts as such things are usually judged, despite the fact that it is considerably younger than the latest known *Allognathosuchus:* Lower Oligocene as against Middle Eocene. If descended from *Allognathosuchus* it is a case of reversion neither impossible nor unique, but not to be accepted without stronger evidence. Granting the reality of the relationships, a more tenable hypothesis would derive the more specialized and more quickly extinct *Allognathosuchus* line and the rather more conservative and tenacious *Caimanoidea* line from a common ancestry. This common ancestry would be characterized chiefly by the short snout, extremely anterior nares, nasals entering but not separating nares, alligatoroid bite, splenials entering symphysis, about twenty teeth in each jaw, of which the fourth and ninth upper and fourth lower were largest, marked tendency towards tooth differentiation into conical anterior and blunt posterior teeth. Most of these characters may also have been present in ancestral alligators. Some of the true crocodiles of the Eocene do not differ very much from this condition, but were advancing in a different direction and with retention of ancestral features lost in these lines.

Mehl (1916) has suggested that *Caimanoidea* is close to the ancestry of *Caiman*. Mook (1923B) does not mention *Caimanoidea*, but advances the structural sequence *Allognathosuchus heterodon, Allog. polyodon, Alligator thomsoni, Allig. sinense, Allig. mississippiensis.* In neither case are these supposed to be direct phyletic lines.

Alligator thomsoni is obviously related to the living species of that genus and particularly to *A. sinense*, as shown by Mook. Relationships to *Caimanoidea* or, still more, to *Allognathosuchus* are speculative at present. The relationship is certainly not direct descent, but it seems

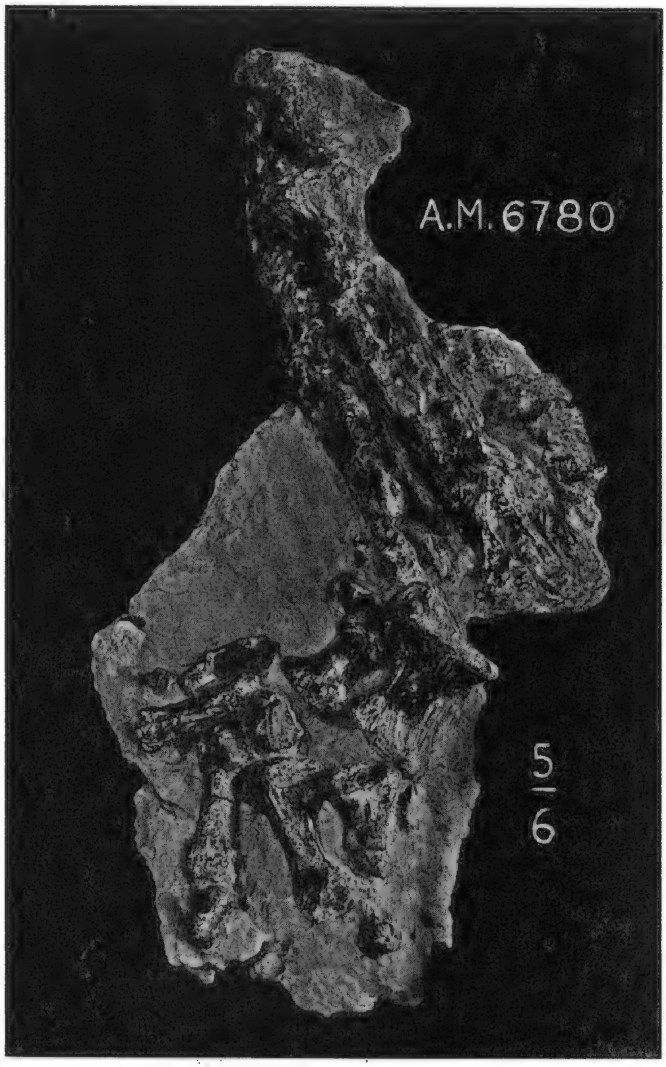

Fig. 6. *Allognathosuchus mooki*, n. sp. Type, Amer. Mus. 6780. Right radius, ulna, carpus, and part of manus, five-sixths natural size.

quite probable that *Caimanoidea* is structurally near the ancestry of *Alligator*, probably nearer than *Allognathosuchus* is to either.

Without prejudicing the results of more detailed study, this preliminary survey suggests the existence in Tertiary times of three alligatoroid offshoots from the crocodile stem type. The first, most divergent

and farthest from the true alligators, is exemplified by *Allognathosuchus*. The second, less aberrant and probably significantly closer to the alligators, is seen in *Caimanoidea*. The third includes the alligators, strictly speaking.

Case (1925) proposed a family, Allognathosuchidæ, defined by the shape of the jaw, grouping of the teeth, and presence of low, blunt teeth adapted to a durophagous diet. These are all intensifications in quantity of characters qualitatively present in various true Crocodilidæ. Their accentuation here is hardly of family value. Apropos of the blunter teeth and presumable difference in diet (the chief basis for family distinction), it is well known that these may be of little or no taxonomic value among modern reptiles. The osteology of *Allognathosuchus* has not more than generic distinctiveness.

STRATIGRAPHIC SIGNIFICANCE

Allognathosuchus has some bearing on the great problem of Cretaceous-Tertiary transition (see especially Matthew 1921). The excellence of this specimen will afford future opportunitites for close comparisons with Cretaceous and Eocene species not yet so well known. It belongs to one of the few families that range over the Paleocene from Cretaceous to undoubted Tertiary. It also belongs to the still smaller group of genera surviving from the Lower Paleocene to Middle Eocene.

At present the line of development to which it belongs is unknown in the Lance or earlier beds, but represented in Wasatch and Bridger by very closely related species. This suggests (although far from proving) that it is part of a Puerco immigration surviving far into the Eocene and tends to this extent to link the Paleocene and Eocene, or, rather, to separate the Cretaceous and Paleocene.

Of still greater value would be the discovery in North America of the Cretaceous ancestry of *Allognathosuchus mooki*, for, while it would disprove the preceding tentative conclusion, it might afford an almost unique opportunity to judge the actual evolutionary advance of a single phylum between undoubted Cretaceous, Paleocene, and undoubted Tertiary. At present this ancestry is not recognized, and this negative evidence must be accepted for what it is worth, as suggested in the preceding paragraph.

As an isolated fact, this occurrence has slight value, but it becomes of importance as one more datum to include in future correlations of all the evidence.

PALÆOBIOLOGY

Allognathosuchus presents a peculiar adaptive type. Mook (1921A) stated that "the characters of the skull and jaws [of the Wasatch and Bridger species] indicate an animal of somewhat different adaptations from the normal crocodilians." Case (1925) tasked Mook with undue conservatism and postulated a "durophagous, probably conchifragous diet." Abel (1928) devoted a separate paper to the palæobiology of the genus, concluding that its diet consisted of chelonians, or was "cheloniphage."

Abel's restoration of the lower jaw of *Allognathosuchus polyodon* (the Bridger species) not only goes beyond the evidence of the originals, but also directly contradicts the descriptions on which he was professedly relying. He shows all of the teeth as blunt, and says without qualification that the large teeth of the lower jaw "ebenfalls niedrige, gerundete Kronen aufweisen." This error misses the most interesting adaptive feature of the dentition and vitiates the whole of his extensive argument.

In all species of *Allognathosuchus* the front teeth are conical, of more or less normal crocodilian character, and only the posterior teeth are low and rounded. The most striking feature of this dentition is not the presence of blunt crushing teeth so much as the highly differentiated character of the dentition. In the lower jaw it consists, so to speak, of three pointed "incisors," a large "anterior canine," a series of quite small intermediate teeth, one or two large, pointed "posterior canines," and a series of crushing cheek teeth of different form from those preceding them. Abel's description of the relative sizes of the posterior teeth is also quite incorrect.

Instead of a single anterior "Brechscherenapparat," there is a more complex and mechanically more sound arrangement. The anterior apparatus, itself complex, is primarily a grasping device. Here the jaws move more rapidly (i.e., in a larger arc) and less powerfully. The posterior apparatus, itself simple, is a crushing device. Here the jaws move less rapidly and more powerfully.

Case's belief in a "conchifragous" and Abel's in a "cheloniphagous" diet may both be discarded as based in the one case on incomplete knowledge and in the other on erroneous premises. The primary inferences, those beyond reasonable doubt, are, first, that the jaws are unusually powerful, with large muscles and functioning as levers with relatively short weight arms, and, second, that the dentition served two localized purposes: (1) grasping and tearing, and (2) crushing.

In the attempt to draw further inferences, necessarily increasingly uncertain, the first point is that this adaptation is not as unusual as both Case and Abel imply, and that Mook's conservatism is more to the point than they grant. In the shape of the snout, in the nature of the bite, in the dual differentiation of tooth shape and function, and in the development of blunt posterior teeth, certain of the short-snouted crocodiles and caimans and, to a less degree, even the alligators do approach this type. In *Osteolæmus tetraspis*, for instance, the front teeth are conical, while the back teeth are very close to those of *Allognathosuchus* in form, and in *Jacare niger* conditions are rather similar. In fact, *Allognathosuchus* merely represents the extreme development of an adaptive type still common although in less specialized form. So far as I have been able to learn, these modern forms are not specialized for one particular and unusual type of diet but are among the *least* specific in food habits, eating birds and mammals and otherwise varying the primarily piscine regimen of their allies.

This is the conclusion that might have been drawn from *Allognathosuchus* itself, even without the aid of analogy. The combination of functions in its dentition does not so much imply limitation as versatility. There seems little either in morphology or analogy to suggest a molluscan diet. Nor with a correct understanding of the dentition can it be justly claimed as "cheloniphagous." Chelonians were perhaps included among other food sources, but apparently were not the sole or principal prey.

Even with the correct data now available, it would be temerarious to push inference farther, but a frankly hypothetical suggestion is possible. As long ago as 1879, Owen suggested a correlation between short- and broad-snouted crocodiles and the rise of mammals. *Allognathosuchus* was a preëminently short-snouted genus, and its rise contemporaneously with the first great expansion of varied and fairly large mammals may not have been wholly fortuitous.[1]

[1]Kellogg's recent study of the food of alligators (U. S. Dept. Agriculture, Technical Bulletin No. 147, 1929) shows mammals as constituting less than 6 per cent. of this food. Birds, reptiles, fishes, insects, and crustaceans each seem as important as mammals in the crocodile diet. A more varied source of data would doubtless alter the exact figures, but it is clear that alligator food habits are highly varied. These concrete observations seem of more value in considering the somewhat analogous *Allognathosuchus* than any amount of theorizing from tooth form to a specific item of diet.

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